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General aspects of the ecology and biogeography of *Artemia*

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Content

Introduction

The present knowledge on brine shrimp in the natural environment is extremely poor ; the number of people involved in ecological *Artemia* research is very limited and as a consequence the number of scientific papers published on *Artemia* ecology is very restricted. Among the

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2 700 papers of the recently updated *Artemia* bibliography (Sorgeloos *et al.*, 1980) it is hard to find more than 50 articles which are strictly ecologically oriented. Collins (1977) is right when he points out that "... considering *Artemia*'s commercial importance as a tropical fish food, its possible utility in aquaculture and the voluminous literature on its physiology, development and behavior in the laboratory, why do we not have dozens of field studies on *Artemia* ?"

From the many branches of science for which *Artemia* has become a most useful study object, ecology is without any doubt the least practiced. This is the more amazing when one considers that further progress of *Artemia* research in physiology, genetics, biochemistry, radiobiology, and not the least in the practical use of brine shrimp in aquaculture, will be dependent to a large extent on our knowledge of the ecology of brine shrimp populations in their natural habitats.

In this review, we shall try to make a synthesis of the present knowledge on *Artemia* as related to its natural environment. We will comment on the many factors (and the complexity of their interactions) which limit and control the presence, the thriving or the disappearance of *Artemia* populations.

Geographical distribution

Decades ago *Artemia* has been recorded from over 80 saline habitats in many countries on the five continents (Abonyi, 1915 ; Artom, 1922 ; Stella, 1933 ; Mathias, 1937). However, many of the ancient salt pans, salt lakes and salt works where brine shrimp were reported to occur, have been destroyed or abandoned : *e.g.* brine shrimp are not found any more in Germany, Great Britain, and Yugoslavia.

With the aid of the available literature and through personal contacts, we have tried to make up the list of all the recent *Artemia* find-spots (Table I through VII). However impressive this listings might appear, they are but provisional and tentative. In most countries no specific *Artemia* survey work has been undertaken yet. The few distribution studies on brine shrimp in the Saskatchewan province in Canada and in Spain resulted in long lists of brine shrimp habitats for these countries (Saskatchewan Fisheries Laboratory, Dr. Atton, personal communication respectively Amat Domenech, 1980).

The recent find-spots of *Artemia* are scattered throughout the tropical, subtropical, and temperate climatic zones, along coastlines as well as inland, sometimes at hundreds of miles from the sea. Although it would seem logical to characterize the coastal brine shrimp biotopes as thalassohaline and the inland ones as athalassohaline, this terminology in fact refers to the chemical composition of the water of the *Artemia* habitat.

Thalassohaline waters are concentrated seawaters (so-called chloride waters) with NaCl as major salt. They make up most, if not all, of the coastal *Artemia* habitats where brines are formed by evaporation of seawater in land-locked bays or lagoons, well-known under the common name of salt pans. During the dry season extensive parts of the shallow lagoons turn into salt flats, many of which in ancient times were transformed by man into solar salt works for salt production. There are, however, also *Artemia* habitats of the thalassohaline type which are located inland, the best known example of this type being the Great Salt Lake in Utah, USA.

TABLE I

Recent *Artemia* find-spots in Africa

Country	Locality
Algeria	Chegga Oasis
	Chott Djeloud
	Chott Quargla
	Dayet Morselli
	Gharabas Lake
	Sebket Djendli
	Sebket Ez Zemouk
	Sebket Oran
Egypt	Wadi Natrun
Kenia	Elmenteita
Libya	Mandara
	Ramba-Az-Zallaf, Fezzan
	Oum el Mâ
	Trouna
	Gabr Aoûn
Madagascar	Salins de Diego
Morocco	Larache
	Moulaya estuary
	Oued Ammafatma estuary
	Oued Chebeica estuary
	Sebket Bon Areg
	Sebket Zima
Mossambica	Nhamaiane
Nigeria	Teguidda-In-Tessoun
Senegal	Dakkar
	Lake Kayur
	Lake Retba
Tunisia	Chott Ariana
	Chott el Djerid
	Sebket Kourzia
	Sebket Sidi el Hani
South Africa	Coega Salt Flats
	Swartkops

TABLE II

Recent *Artemia* find-spots in Australia

Country	Locality
Central Queensland	Port Alma
	Bowen
	Rockhampton
New Zealand	Lake Grassmere
Southern Australia	Dry Creek Saltfields, Adelaide
Western Australia	Dampier
	Lake McLeod
	Port Hedland
	Rottnest Island
	Shark Bay

Table III

Recent *Artemia* find-spots in North America

Country		Locality
Canada		Akerlund Lake
		Alsask Lake
		Aroma Lake
		Berry Lake
		Boat Lake
		Burn Lake
		Ceylon Lake
		Chain Lake
		Chaplin Lake
		Coral Lake
		Drybore Lake
		Enis Lake
		Frederick Lake
		Fusilier Lake
		Grandora Lake
		Gull Lake
		Hatton Lake
		Horizon South
		Ingerbright North
		Landis Lake
		Little Manitou Lake
		Lydden Lake
		Mawer Lake
		Meacham Lake
		Muskiki Lake
		Neola Lake
		Oban lake
		Penley Lake
		Richmond Lake
		Shoe (Horseshoe) Lake
		Snakehole Lake
		Sybouts Lake – East
		Sybouts Lake – West
		Verlo East
		Vincent Lake
		Wheatstone South
		Whiteshore Lake
USA	Arizona	Long H. Lake
		Kiatuthlana Red Pond
		Kiatuthlana Green Pond
	California	Carpinteria Slough
		Elkhorn Slough
		Mono Lake
		Moss Landing
		San Diego
		San Francisco Bay
		San Pablo Bay
		Vallejo West Pond

Country	Locality
USA Hawaii	Laysan Atoll
Nebraska	Alkali Lake # 2
	Ashenburger Lake
	Cook Lake
	East Valley Lake
	Grubny Lake
	Homestead Lake
	Jesse Lake
	Johnson Lake
	Lilly Lake
	Reno Lake
	Richardson Lake
	Ryan Lake
	Sheridan County Lakes
Nevada	Big Soda Lake
North Dakota	Miller Lake
	Stink (Williams) Lake
New Mexico	Quemado
	Zuni Salt Lake
Texas	Playa Tahoka
Utah	Great Salt Lake
Washington	Hot Lake
	Omak Plateau

TABLE IV

Recent *Artemia* find-spots in Central America

Country	Locality
Bahamas	Great Inagua
	Long Island
Martinique	
Mexico	Baja California
	Pichilingue Island
	San Jose Island
	Yavaros
Netherlands Antilles	Aruba
	Bonaire Gotomeer
	Pekelmeer
	Slagbaai
	Curaçao
Puerto Rico	Bahia Salinas
	Bogueron
	La Parguera
	Tallaboa
Santo Domingo	
St. Martin	

TABLE V

Recent *Artemia* find-spots in South America

Country	Locality
Argentina	Bahia Blanca
	Buenos Aires
	Carahue
	Hidalgo
	Mar Chiquita
	La Pampa
Bolivia	
Brazil	Cabo Frio
	Macau
Chili	
Colombia	Galera Zamba
	Manaure
Ecuador	
Peru	Callao
	Caucato, Pisco
	Chilca, Lima
Venezuela	Coro Coastline
	Los Roques
	Boca Chica Salt Lake
	Port Araya
	Salinas Grandes de Hidalgo
	Tucacas

TABLE VI

Recent *Artemia* find-spots in Asia

Country	Locality
China	Tientsin
	Tsjingtao
India	Bhayander, Bombay
	Jamnagar
	Karsewar Island
	Kutch
	Sambhar Lake
	Tuticorin
	Vadala, Bombay
Iraq	Abu-Graib, Baghdad
Iran	Lake Rezaiyeh
	Schor-gol
Israel	Eilat North
	Eilat South
	Kalia potash works (Dead Sea)
	Solar Lake
Japan	Chang dao
	Yamaguchi, Seto Naikai
Turkey	Çamalti saltern, Izmir

TABLE VII

Recent *Artemia* find-spots in Europe

Country	Locality
Bulgaria	Burgas Salt Works
	Pomorije Salt Works
Cyprus	Akrotiri Salt Lake
	Larnaca Lake
France	Aigues Mortes
	Carnac – Trinité sur Mer
	Guérande – Le Croisic – La Boule
	La Palme
	Mesquer – Assérac
	Salin du Giraud
	Sète
	Lavalduc
Italy	Comacchio
	Margherita di Savoia
	Sicily
Portugal	Alcochete
	Tejo estuary
	Sado estuary
	Ria de Aveiro
	Ria de Faro
Roumania	Lake Techirghiol
Sardinia	Cagliari
	San Bartholomeo
	Santa Gilla
Spain	Armalla
	Ayamonte
	Barbarena
	Cabo de Gata
	Cadiz – San Felix
	– San Fernando
	Calpe
	Campos del Puerto, Mallorca
	Delta del Ebro
	Gerri de la Sal
	Imon
	Isla Cristina
	Janubio, Lanzarote
	Laguna de la Playa Bujaraloz
	Laguna de Quero
	Lepe
	Lerin
	Medinaceli
	Molina del Segura
	Peralta de la Sal
	Poza de la Sal
	Rienda
	Roquetas
	Saelices

Country	Locality
Spain	Salinera Catalana
	Salinera Espanola, Formentera
	Salinera Espanola, Ibiza
	Salinera Punta Galera
	Salinera San Antonio
	Salinera San Felix
	San Juan del Puerto
	Sanlucar de Barrameda
	San Pedro del Pinatar
	Santa Pola – Bonmati
	– Bras de Port
	– Salinera Española
	Siguenza
	Villena
USSR	Bol'shoe Otar – Mojnaskoe
	Burlinskoe
	Dzharylgach
	Ghenicheskoyo Lake (Herson)
	Kuchukskoe
	Kujalnic estuary
	Odessa
	Petukhouskoe
	Popovskoe Lake
	Sakskoe
	Sasyk Lake (Sivash)
	Sasykul Lake (Pamir)
	Tabichigskoe Lake
	Tambukan
	Toberchicskoe Lake

Athalassohaline *Artemia* biotopes are all located inland and are characterized by an ionic composition that differs very much of that of natural seawater. There are sulphate waters (*e.g.* Chaplin Lake in Saskatchewan, Canada ; Hammer *et al.*, 1975), high carbonate waters (*e.g.* Mono Lake in California, USA ; Mason, 1967), and potassium-rich waters (several of which are located in Nebraska, USA ; Cole and Brown, 1967).

As far as the size of *Artemia* biotopes is concerned, brine shrimp occur as well in very large biotopes (Lake Rezaiyeh, formerly lake Urmia, in Iran, with a surface of approximately 6 000 km^2 ; Löffler, 1961) as in small salt ponds such as Solar Lake in Israel, that has a surface of only a few hundreds of m^2 (Por, 1968).

Most of the coastal *Artemia* biotopes are very shallow, with minimal physical, chemical or biological stratification. Some of the inland *Artemia* habitats on the contrary, are relatively deep and stratified, such as Mono Lake in California, USA (Dana *et al.*, 1977).

Notwithstanding the cosmopolitan character of the occurrence of *Artemia*, it appears, when taking a closer look at the regional level, that its distribution is discontinuous in many places of the world. In other words, *Artemia* does not occur in every existing body of saltwater. The main reason for this is that *Artemia* cannot migrate from one saline biotope to another via the

seas, because it does not have any anatomical defense structure against predation by carnivorous aquatic organisms, *e.g.* larger crustaceans and fish. The principal dispersion mechanism of *Artemia* is transportation of cysts by wind and by waterfowl, as well as deliberate human inoculation in solar salt works. The fact that in most cases the cysts float at the surface of the water lays at the basis of transportation both by wind and waterfowl. The cysts either adhere to the feet and the feathers of the birds which come down on the water or they are washed ashore where they dry and are carried away by the wind.

Flamingos and some species of seagulls and ducks contribute to the geographical distribution of *Artemia* strains not only by external transportation but also via the ingestion of food. Some of these birds feed indeed on live brine shrimp (which may have cysts in their uterus) or on cysts washed ashore. It has been demonstrated (Horne, 1966 ; MacDonald, 1980) that part of the cysts ingested withstand digestive enzymes and are excreted without having lost their viability. Löffler (1964) has shown experimentally that *Artemia* cysts can remain intact for 3 days in the digestive tract of birds and during this period some types of birds (*e.g.* flamingos) can cover more than 1 000 km. An example of possible long-distance transportation can tentatively be extrapolated from the findings of Bowen *et al.* (1978). These authors discovered that the brine shrimp in the salterns of Kutch in north India and those of Madras[4] in south India are genetically identical. Most probably this is the result of transportation of this specific strain by flamingos which migrate between the salt pans of both areas.

The absence of a migration route of birds is probably the reason why the very large salinas along the northeast coast of Brazil are not inhabited by brine shrimp, with the exception of the Macau salt works where *Artemia* was inoculated by man in one saltern just a few years ago (see further).

The deliberate inoculation of *Artemia* in solar salt works by man has been a current practice in the past. The presence of brine shrimp in salterns indeed seems to have a positive influence on the production of seasalt (Davis, 1977). Geddes (1980) mentions that all *Artemia* populations recorded in Australia have probably been imported by man. The strains occurring in Shark Bay in Western Australia and those in Rockhampton in Queensland are indeed very similar to the San Francisco Bay (California, USA) strain (Bowen *et al.*, 1978 ; Abreu-Grobois and Beardmore, 1980).

Ecological characteristics

Tolerance levels

Temperature

Most geographical strains do not seem to survive at temperatures below 6 °C unless of course under the form of cysts. The maximum temperature that *Artemia* populations tolerate has repeatedly been reported to be close to 35 °C, a temperature which is often attained in the shallow tropical salterns that constitute a large part of the *Artemia* habitats. This tolerance

[4] According to Royan (personal communication) the Madras *Artemia* are in fact populations from the Tuticorin salterns in India.

treshold is, however, strain-dependent. Recent inoculation tests in Thailand revealed that, after a certain adaptation period, brine shrimp from Macau (Brazil) survived for weeks at temperatures around 40 °C (Vos and Tansutapanit, 1979). As far as the optimum temperature is concerned there are probably as many temperature optima as there are *Artemia* habitats. The growth of animals in nature is indeed influenced by the entire set of abiotic and biotic factors of the environment in which it lives. On the basis of all data available it is, however, probably no heresy to claim that the optimum for *Artemia* must be situated in the range from 25 °C to 30 °C.

The ametabolic dehydrated cysts resist to a much wider temperature range, which is never occurring in nature ; *i.e.* the minimum being the absolute zero (-273 °C ; Skoultchi and Morowitz, 1964) and the maximum close to 100 °C (Hinton, 1954).

Ionic composition of the medium

Artemia can withstand environments in which the ratio of the major anions and cations is not only totally different from that in seawater but reaches extreme values (inferior as well as superior) in comparison to natural seawater. The Na^+ to K^+ ratio which is 28 in seawater attains 8 respectively 173 in some *Artemia* habitats : that of Cl^- to CO_3^{2-}, which is 137 in seawater may decrease to 101 and reach 810 at the other extreme ; the Cl^- to SO_4^{2-} ratio which is 7 in seawater has been reported to be 0.5 respectively 90 in certain *Artemia* biotopes (Cole and Brown, 1967 ; Bowen *et al.*, 1978). This striking physiological adaptation to such extreme chemical habitats, already described by several biologists at the beginning of this century, made Cole and Brown (1967) conclude that "... the ionic composition of the waters inhabited by *Artemia* varies more than that of any other aquatic metazoan".

Salinity

As far as the upper limit of salinity is concerned, brine shrimp have been found alive in supersaturated brines at salinities as high as 340 ‰ (Post and Youssef, 1977). It is, however, quite understandable that under these extreme conditions the animals barely manage to survive and do no longer assume most of their normal physiological and metabolic functions.

The lower salinity limit in which *Artemia* is found in nature, is in most cases function of the presence of predating animals. Brine shrimp are indeed very seldom found in waters with a salinity lower than 45 ‰, although physiologically they thrive in seawater and even in brackish waters. As a general rule, we may say that the lowest salinity at which *Artemia* is found in nature varies from place to place and is determined by the upper salinity tolerance-level of the local predator(s). Hedgpeth (1959) mentioned that for several species of marine fish and invertebrates this level can be as high as 80 to 100 ‰ ; some fish species even seem to survive in salinities above 100 ‰ and even up to 130 ‰.

As is the cause for temperature, there is no well-defined optimum for salinity ; for physiological reasons, this optimum must, however, be situated towards the lower end of the salinity range. Indeed the higher the salinity, the more energy *Artemia* must spend for its osmoregulation.

An important aspect of salinity in the life cycle of brine shrimp is the effect of this physicochemical factor on the metabolism of the cysts. *Artemia* cysts will start to develop when the salinity of the medium drops below a certain treshold value, which is strain dependent (*e.g.*

85 ‰ for the San Francisco Bay strain). At salinities above this treshold *Artemia* cysts will never hatch because they cannot hydrate enough, which is one of the perequisites for the onset of the hatching metabolism.

Oxygen

Artemia is a typical euroxybiont since it has been reported to survive in environments with less than 1 ppm dissolved oxygen and, at the other extreme, in situations where algal blooms increase the oxygen level beyond 150 % saturation. The optimal oxygen concentration, though unknown, must logically be close to the saturation level.

pH

Although in nature brine shrimp are found in neutral to alkaline waters, very little is known about the influence of the pH on juveniles or adults. For the cysts it is important to note that the hatching efficiency decreases when the pH drops below 8 (Sato, 1967).

PHYSIOLOGICAL ADAPTATION MECHANISMS

As already said, brine shrimp do not possess any anatomical defense mechanism against predation and *Artemia* populations are always in danger at salinities which are tolerated by carnivorous species. Brine shrimp, however, have developed a very efficient ecological defense mechanism by their physiological adaptation to media with very high salinity. As such they can escape from their predators thanks to this salinity barrier.

Although brine shrimp possess the best osmoregulation system known in the animal kingdom, the fact that they thrive in media with a high salinity means that at the same time they have to live in environments with low oxygen levels (the saturation value for oxygen indeed being inversely proportional to the salinity level). At the exception of short periods of oversaturation of eutrophic waters during the day, *Artemia* usually has to cope with low oxygen concentrations. Brine shrimp are weapened against this unfavorable environmental condition by their capability of synthesizing very efficient respiratory pigments. The concentration of these haemoglobins increases with increasing salinities, thus with decreasing dissolved oxygen levels.

The third ecological adaptation mechanism is the ability of *Artemia* to assure the survival of the species by formation of encysted, ametabolic embryos or cysts which resist better to extreme environmental conditions than do the juveniles and the adults. There are many theories about the exact mechanisms which control the onset of cyst formation in brine shrimp. The latest information points to the major role which oxygen fluctuations or more exactly fluctuations in the redox-potential of the water seem to play in this mechanism (Versichele and Sorgeloos, 1980).

Artemia cysts will stay in diapauze as long as the salinity of the medium remains above the hatching treshold. Decreases of the salinity in brine shrimp habitats mostly occur on a cyclic or seasonal basis by rainfall or runoff of freshwater in the biotope. As said before, whenever the salinity drops to a value below the hatching treshold a new brine shrimp population can develop. It should be emphasized that situations of a temporary low salinity often occur in a salt lake, *e.g.* the restricted area of inflowing freshwater, or after rainfall when for a while a freshwater layer remains on top of the heavier salt water.

Another proof that brine shrimp have an extreme adaptability to salinity stresses is that nauplii which hatch out of cysts in a water layer of very low salinity (down to 5 ‰) survive very well when this water layer is mixed by wind action or currents with waters of very high salinity. This phenomenon was probably overlooked by Royan *et al.* (1978) when they extrapolated from salinity readings in nature that cysts had hatched in media of 130 to 160 ‰ salinity.

It seems appropriate to make here a small digression about the great advantage which brine shrimp have conserved during their developmental history in comparison to freshwater anostracan crustaceans, such as *Chirocephalus* and *Streptocephalus*. Freshwater anostracans have lost the capability of producing live offspring. This can be seen as an adaptation to their natural habitat (ephemeral ponds, *i.e.* temporal biotopes) characterized by cyclic successions of drying out completely and being refilled after a certain time by rainfall. Since the aquatic phase of the cycle is in most cases rather short (from a few weeks to a few months) the animals, after hatching, have merely the time to grow out into one generation of adults which form cysts in order to resist to the dry period. As a result, in nature one seldom encounters dense populations of freshwater anostracans.

The *Artemia* cycle is quite different. When the conditions required for hatching are fulfilled, the cysts hatch into nauplii which grow in a few weeks to adults. Since most *Artemia* habitats are perennial, a dual mode of reproduction has an adaptive value : through ovoviviparity a small number of adults give rise to a fast population explosion leading to very high densities of animals, very typical for *Artemia* biotopes. It is only when the environmental conditions arrive at a certain critical treshold that ovoviviparity shifts to oviparity with formation of cysts.

Feeding characteristics

Brine shrimp are typical filter-feeders, ingesting particulate material of a size range which laboratory experiments have shown to extend from a few micrometer up to approximately 50 micrometer. Since the continuous beating of the thoracopods carried out by the animal for respiration serve at the same time to collect food particles, *Artemia* does not have any choice but to feed continuously.

The food consumed by *Artemia* in nature is made up of varying percentages of inert particulate material of biological origin (organic detritus) and living organisms of the appropriate size-range (mostly microscopic algae and bacteria).

In many *Artemia* biotopes the presence of high numbers of brine shrimp often coïncides with blooms of microscopic algae (green algae, blue green algae, diatoms, *etc.*). The richness in dissolved or particulate organic matter of these blooming waters in turn promotes the development of large numbers of heterotrophic bacteria.

The presence of algal material in the gut or the intestine of brine shrimp should not be considered as an evidence of its nutritional value nor of its digestibility for *Artemia* ; experiments performed by Reeve (1963) and Dobbeleir *et al.* (1980) have indeed shown that *Artemia* even ingests sand grains or glass microspheres.

As far as competition for food is concerned, *Artemia* does not seem to have competitors in the high salinity waters. The brine fly *Ephydra*, often encountered in large numbers in *Artemia* biotopes, is more a benthic feeder and does not interfere with the *Artemia* food chain.

At the lower end of the salinity range brine shrimp, however, must suffer the presence and competition for food of several groups of invertebrates, such as rotifers, ciliates, and other crustaceans (anostracans and copepods).

PREDATION

As already mentioned, *Artemia* populations are subject to serious predation in all situations where the predator can withstand the salinity of the medium. The list of *Artemia* predators thus includes per definition all species feeding on zooplankton that populate natural seawaters. Since this list comprises as well all tropical fish, prawn, shrimp, lobster and fish species which one now endeavors to mass culture on a controlled basis, we find here the major reason for the great interest which aquariologists and aquaculture people show for *Artemia*. In typical *Artemia* habitats (thus at higher salinities) several categories of insects regularly predate on brine shrimp : Odonata larvae, aquatic Hemiptera and Coleoptera ; some of the hemipteran families Corixidae and Notonectidae can withstand very high salinities. Mullet, milkfish, and *Tilapia* predate heavily on brine shrimp in salt pans and salt lakes ; some of these fish species can indeed withstand salinities up to 120 ‰. Predators to which *Artemia* cannot escape through the high salinity barrier are of course the birds. For several species of waterfowl *Artemia* constitutes an important part of their diet. Isenmann (1975) reported that in the salt pans of the Camargue (France) little gulls (*Larus minutus*) feed almost exclusively on brine shrimp from March to October. Besides gulls and avocets, flamingos are the group of birds most often quoted to feed on *Artemia* in saltwater bodies (Rooth, 1965). Later we shall comment on the relation *Artemia*-waterfowl and its ecological importance.

PARASITES AND DISEASES

Not much is know about parasites and diseases of *Artemia* in their natural habitats. Scattered throughout the scientific literature it is reported that brine shrimp can be contaminated by viruses, endosymbiontic procaryots, bacteria (spirochaetes), fungi, and flatworms of the group of the Cestodes, but no information is given as to what extent these contaminants affect the populations.

Strain characteristics

Since *Artemia* biotopes are geographically isolated from one another, each habitat can theoretically be populated by a different geographical strain. The study of these strains, especially from the genetic point of view, has already resulted in several most important findings.

The first and not the least important is that the genus *Artemia* consists in fact of several sibling species which are isolated from the reproductive point of view (Kuenen, 1939 ; Barigozzi and Tosi, 1959 ; Clark and Bowen, 1976). As a result we are no longer entitled to refer to *Artemia salina* ; instead we are dealing with *Artemia monica*, *A. tunisiana*, *A. urmiana*, *A. persimilis* or *A. franciscana*[5].

[5] See editioral note on the taxonomy of *Artemia* in this book.

Since the characterization of *Artemia* strains is treated in detail in many papers of these Proceedings, we only mention here that there are bisexual or zygogenetic strains (with males and females) and parthenogenetic strains (only females). Strains also differ in their chromosome number : there are diploid, triploid, tetraploid, pentaploid, and even dekaploid strains.

The large variety among *Artemia* strains in genotypical and phenotypical differences is reflected in a number of features which can be morphological, biometrical, biochemical or physiological. This subject is now investigated in detail by several teams of scientists participating in the International Study on *Artemia* (Sorgeloos, 1980a).

Nutritional differences between geographical strains of *Artemia* are related in the first place to the biochemical composition of the animals which can vary to a large extent between strains growing in different biotopes under the influence of different abiotic as well as biotic factors. For the abiotic factors, all hydrographic and climatological parameters play a role, since they will either have a direct or an indirect influence on the physiology of the brine shrimp. The water temperature for example, which is different from one place to another as a result of the configuration of the biotope as well as of the prevailing climate, is known to influence, at least in part, the biochemical composition of *Artemia* (Hines *et al.*, 1980). The indirect influence which environmental factors exert on the biochemical composition of brine shrimp acts through the food chain. Depending on the local conditions of climate and nutrients, a specific type of food will dominate in each *Artemia* habitat ; this in turn will influence the biochemical composition and thus the nutritional value not only of the adult brine shrimp but also of the embryos and thus of the nauplii which will hatch out of the cysts. In addition, a factor which unfortunately has already proved to have an adverse influence on the nutritional value of brine shrimp is contamination of some *Artemia* habitats with persistent pesticides (Olney *et al.*, 1980).

Productivity of *Artemia* biotopes

Production of nauplii, juveniles, and adults

Collecting information on the quantity of brine shrimp present in a saltwater body, either as number of individuals or as biomass per unit of water or per surface area, is not a very easy task. As a consequence it is not surprising that there are few quantitative data (even approximate ones) in the literature. The origin of this difficulty lays in the fact that *Artemia* is an organism which not only may show a strong phototactic behavior but which as a true planktont cannot overcome water currents created by winds. As a consequence brine shrimp are often swept in patches of very high density from one spot to another. Baker (1966) gave the following pertinent comment on her failure to quantify brine shrimp in salt ponds "... I have visited the ponds, filtered gallons of pond brine, walked around the pond and decided that the population was very small because no shrimp were visible, only to return the next day and find the brine 'boiling' with *Artemia*".

Tentatively we gathered all quantitative estimates on the maximum densities of brine shrimp in different sites, which we could find in scientific papers (Table VIII). No doubt commercial harvesters of brine shrimp could add more precise information.

TABLE VIII

Literature data on the productivity of *Artemia* habitats

Site	Country	Maximum production	Period	Author
Lake Rezaiyeh	Iran	1.2 adults/l		Parker (1900)
Sivash Salt Lakes	USSR	400/l		Gun'ko (1962)
Slagbaai	Bonaire, Netherlands Antilles	200-360/l	Oct.-June	Rooth (1965)
Mono Lake	California, USA	4 adults/l 12 nauplii/l 400/l	June-Sept. Aug.-Sept.	Mason (1967) Lenz (1980)
Great Salt Lake	Utah, USA	10/l		Wirick (1972)
Salin de Giraud	Camargue, France	10-100/l 0.02-0.2 g/l wet weight	March-Oct.	Isenmann (1975)
Long Island salina	Bahamas	25-100/l	May-Sept.	Davis (1978)
Alviso Salt Ponds	California, USA	13 g/m³ dry weight	summer	Carpelan (1957)
San Francisco Bay Salt Ponds	California, USA	5 kg/ha wet weight (harvest)	per week	Baker (1966)
Crimea Salt Lakes	USSR	250 kg/ha 3 000 kg/ha	October June	Voronov (1973)
Burgas-Pomorije Salt Works	Bulgaria	2.75 g/l adults wet weight 0.93 g/l juveniles 0.05 g/l nauplii	June-Sept.	Lüdskanova (1974)

A closer look at the *Artemia* biomass-data reveals that :

1) different authors use different standards to express their results ; intercomparison is extremely difficult if not impossible ;
2) the productions which are expressed in identical units vary very much from one site to another and even within the same biotope between different samplings ;
3) some authors report extremely high productivities : the 3 000 kg/ha (probably wet weight figure) given by Voronov (1973) for the Crimea Salt Lakes in the USSR during June, means a production of 300 g/m^2 which most probably is a hazardous extrapolation to the entire biotope of a few samplings in a patch of *Artemia*.

It should be reminded that the distribution of brine shrimp over the entire habitat is seldom homogenous and that as a consequence it is extremely difficult to calculate exact productions. The best method of approximation should always be to sample at different moments, in as many places as possible, by vertical plankton hauls, and then calculate the average for the entire biotope.

Whatever the data presented here are worth, the *Artemia* productivity is definitely associated with the primary productivity and/or with the richness in particulate organic matter.

During the 4th World Symposium on Salt Production, Davis (1977) reported on the positive influence which micro-organisms (algae or bacteria) exert on the production of salt

and concluded that the most productive salinas (from the point of view of salt production) are those where the inflowing water is rich in the essential nutrients nitrogen and phosphorus. According to this author salt works should best be located as close as possible to "mineral rich" areas, such as population centers, river mouths, deep water and ocean upwellings. From his statement we can deduce that the most productive salt works will also be the most productive *Artemia* biotopes. With regard to this, it is interesting to mention the reciprocal benefit of the predator-prey relationship between *Artemia* and waterfowl, especially flamingos. As said earlier, saline biotopes are much visited by waterfowl which feed on brine shrimp, but these birds in turn fertilize the biotope with their guano, contributing in this way to the productivity of the ecosystem by a feedback mechanism.

We would like to add from our own experience, a fifth category to the list of most productive salinas (thus most productive *Artemia* biotopes) proposed by Davis (1977), namely the solar salt works which receive their intake waters from a mangrove area. A good example of this category are the salt works of Macau in Brazil. Since their recent inoculation with a small quantity of brine shrimp, these salt works in northeastern Brazil became one of the most productive *Artemia* biotopes in the whole world.

Production of cysts

Most *Artemia* strains produce cysts that float. In Mono Lake (California, USA), however, the local sibling species *Artemia monica* produces cysts that sink. As a result the classic dispersion mechanism does not take place and the latter strain is, from the biogeographical point of view, much more isolated than brine shrimp strains which produce floating cysts.

We have tried to make up a table of existing data on the production of cysts in *Artemia* habitats (Table IX). A thorough literature search revealed only four papers with data on this matter. Since we know from wholesalers that the quantity of cysts which are sold annually must now be close to 100 tons, we can but wonder about the scant scientific information on cyst production in different countries. From the table one can of course not conclude very much ; according to our own estimations a good *Artemia* biotope produces some 10 to 20 kg of cysts per hectare per season.

Table IX

Literature data on the production of cysts in *Artemia* habitats

Site	Surface	Country	Harvest	Author
Marina-Salina	1 ha	California, USA	50 kg/year	Boone and Baas-Becking (1931)
Crimea Salt Lakes	70 km²	USSR	32 400/l/year	Voronov (1973)
San Francisco Bay	> 1 000 ha	California, USA	18 kg/ha (4 months per year)	Rakowicz (in Helfrich 1973)
Burgas Pomorije Salt works	550 ha	Bulgaria	from 326 g/m³ to max. 838 g/m³	Lüdskanova (1974)

Exploitation of *Artemia*

The key position that brine shrimp are presently occupying in aquaculture and in aquariology both under the form of cysts and of adults is well-known (Sorgeloos, 1980a).

Adult *Artemia* are mainly collected from shallow salt ponds with conical nets mounted in front of a very small raft or boat equipped with an outboard motor. With this relatively simple technique, Rakowicz (quoted in Baker, 1966) reported a daily harvest of up to 4 tons of fresh weight *Artemia*. The best catches are made on a cloudy morning after a calm night. In such conditions the dissolved oxygen concentration in the highly eutrophic San Francisco Bay salt ponds is so low that the animals concentrate in very dense "blow-ups" to perform surface respiration. These accumulations are so spectacular that they can be seen from small planes flying over the salt ponds.

Another type of harvesting technology takes advantage of the positive phototactic behavior of the brine shrimp, the intensity of which, is, however, strain and temperature dependent.

Apparently no attention has ever been paid to the influence which massive *Artemia* catches may have on the ecosystem of a particular saltwater body. To saveguard the maximum productivity of the *Artemia* habitat from the point of view of production of both adults as well as cysts it is imperative that, in analogy to fisheries, the "maximum sustainable yield" be determined.

To date *Artemia* cysts are harvested at many places in the world (Sorgeloos, 1979, 1980b). They are collected either directly in the water or after being thrown ashore where they accumulate in reddish-brownish layers, several cm thick and many meters in length. The best catches are usually made in sites where the direction of the dominant winds is relatively constant and the cysts are always thrown ashore at the same spot. With unstable wind regimes cysts move around the salt ponds and before they can be harvested they risk to be hydrated and hatch out (*e.g.* in the surface water layer of lower salinity after a period of rainfall). The same can also happen with cysts accumulated on shore. For this reason, and also because dry cysts can be blown away by winds, commercial harvesters should always collect cysts as regularly as possible. From the practical point of view of *Artemia* cysts exploitation, advantage can be taken of the positive influence of the winds for the accumulation of the cysts. Ponds for cyst production should be built very long and quite narrow, with the length axis in the direction of the dominating winds ; the cysts produced will then accumulate at one end of the pond where they can be easily collected (more details on cyst harvesting and processing can be found in Sorgeloos, 1978).

***Artemia* inoculation in saltwater bodies**

Aside from failure of dispersion, adverse climatological conditions, especially in monsoon-climates, are probably also limiting the presence of *Artemia* in saltwater bodies which at first glance look suited for brine shrimp. In South East Asia for example (Thailand, Philippines, Indonesia, *etc.*), where thousands of hectares of salt pans can be found during the dry season, *Artemia* is not naturally occurring. This can be explained by the fact that neither the cysts nor the live brine shrimp could survive throughout the rainy season ; *i.e.* at the low salinities cysts would hatch and all live animals would be eliminated by predating fish and crustaceans.

Considering the important role of *Artemia* in aquaculture today, the question can be raised if we cannot utilize our present knowledge on the biology of the brine shrimp and on the ecology (even if the latter is still relatively poor) to develop *Artemia* farming in natural saltwater bodies.

A promising step in this direction is the artificial inoculation of *Artemia*. The benefits which can be derived from inoculating brine shrimp in salinas where these crustaceans do not occur naturally are obvious : as a result of the high reproductive capacity of brine shrimp, a small inoculum of nauplii in highly productive salt ponds at salinities around 120 ‰ and water temperatures in the range from 25 to 35 °C, will lead to a fast population explosion. In salinas managed for salt production animals will be drained from one evaporation pond to another and cysts will be produced in the higher salinity ranges ; in man-managed *Artemia* ponds, salinity conditions can be controlled at will as to favor the production of either *Artemia* biomass or cysts.

A distinction should be made here between definitive and temporary inoculations. Definitive inoculations are those where one single inoculation will lead to the permanent establishment of an *Artemia* population. A first attempt in colonizing natural saltwater bodies with *Artemia* has been tried out in the early seventies in hypersaline lagoons on Christmas Island in the Central Pacific (Helfrich, 1973). This inoculation has not been very successful for two major ecological reasons :

1) the salinity is too low in most of the ponds to protect the developing brine shrimp populations against predation by several fish species ;
2) although one had hoped to be able to enrich the intake waters in order to permit the development of a substantial phytoplankton biomass, this has not been the case. Helfrich (1973) indeed concluded that "... without enriching the Christmas Island waters there is presently insufficient phytoplankton productivity potential to support the proposed *Artemia* culture scheme".

Artificial nutrient enrichment with fertilizers, which could have been a practical solution for the second obstacle, was unfortunately not feasible because the transport of inorganic nitrogen and phosphor salts to this isolated and desert atoll island in the Pacific was economically prohibitive.

More recent experimental inoculations have been carried out in Macau (Brazil) and in Cuba. The seeding of one salt pond in a very large salt work in Macau (Rio Grande do Norte, Brazil) with nauplii hatched out of 250 g of San Francisco Bay (California, USA) cysts has been extremely successful. All prerequisites for a mass development of *Artemia* were fulfilled and brine shrimp spread out over the 3 000 ha solar salt works. The first kg of cysts was harvested after only a few months after inoculation. Present harvests exceed 20 metric tons per year (for a harvesting period from September through March, Van Tilburg, personal communication). It is interesting to note that neighboring salt works have been inoculated with *Artemia* through dispersion from Macau by local waterfowl.

As far as temporary inoculations are concerned, successful trials have been made during the dry season in the Philippines (de los Santos *et al.*, 1980), in Thailand (Vos and Tansutapanit, 1979) and in India (Royan, personal communication). Water levels in these salt ponds were increased from a traditional level of less than 10 cm to 25 cm or more in order to keep temperatures around or below 35 °C during the hotest moment of the day. Extrapolated

from the production figures obtained so far, average cyst harvests amounted to approximately 20 kg/ha and per season. Experiments are now in progress in Thailand to test the possibility of increasing *Artemia* productions by application of organic manure, *e.g.* duck and chicken dung (Tansutapanit, personal communication).

Temporary inoculations offer a number of biological advantages in comparison to definitive inoculations. The former permit to experiment with different *Artemia* strains in order to find the strain that is best adapted to the local conditions. A bad choice is in this case less of a disaster than with a definitive inoculation, since the *Artemia* population is only established temporarily. Furthermore temporary inoculations offer unique possibilities for fundamental experimentation in natural salt ponds, *e.g.* with regard to genetical stability and phenotypical characteristics of the numerous geographical strains of brine shrimp from which cyst material is now available.

Perspectives of brine shrimp production in nature

To conclude this review we would like to turn to the future and look at the tremendous potential of controlled *Artemia* production in natural sites found at many places around the world ; *i.e.* thousands of hectares of abandoned salterns as well as the large flats along estuaries and mangrove areas. Part of the latter sites can easily be transformed by the construction of dikes into evaporation ponds ; when properly managed from the point of view of temperature and salinity, these ponds can produce thousands of tons of *Artemia* biomass either on a continuous or on a cyclic basis.

Finally we want to make a strong plea for the preservation and saveguarding of all existing natural *Artemia* habitats. Salt lakes and salt ponds are unique and well-balanced ecosystems of which man can easily destroy the very particular food chain including *Artemia* and migrating birds. We should be aware, that if we destroy the original *Artemia* gene pools we condemn at the same time our basic potential of genetic improvement and cross-breeding of *Artemia* strains. And this, exactly as in any type of farming and husbandry, would be the biggest drawback for all the hopes which we are placing today in the advancement of aquaculture and the mass culturing of *Artemia* as a most wellcome addition to the production of animal protein.

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